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Evaluation of Genetic Traits for Improving Productivity and Adaptation of Groundnut to Climate Change in India

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Abstract

Anticipated climate change will alter the temperature and rainfall characteristics of crop growing seasons. This will require genetic improvement of crops for adapting to future climates for higher yields. The CROPGRO model for groundnut was used to evaluate genetic traits of Virginia and Spanish types of groundnut for various climate scenarios of India. The analysis revealed that productivity of groundnut can be increased in current and future climates by adjusting the duration of various life-cycle phases, especially the seed-filling to physiological maturity (SD-PM). Increased maximum leaf photosynthesis rate (AMAX), increased partitioning to reproductive organs (XFRT) and increased individual seed-fill duration (SFDUR) all contributed to the increase in pod yield in all climates. More determinate pod set (shorter PODUR) was beneficial only in the water deficit environments. The positive effect of increasing specific leaf area (SLA) and leaf size (SIZLF) on pod yield was greater in environments more favourable for plant growth. Increasing reproductive tolerance to high temperature by 2 °C increased pod yield of groundnut in warmer environments, especially where the crop often suffers from drought. Increased adaptive partitioning to roots (ATOP) increased drought resistance of groundnut on high water-holding capacity soils. Combination of traits had additive effects and pod yield increased substantially. These results indicate that the CROPGRO model can be used to assess the potential of individual or combination of plant traits for guiding breeding of improved groundnut varieties for current and future climates.

Introduction

Crop growth and yield of a cultivar in an agro-climatic environment is determined by its agronomic management and genetic traits that determine its plant morphology, vegetative and reproductive development, production of biomass and its allocation to different plant organs. These genetic traits interact with environmental factors resulting in different outcomes in terms of growth and yield in different environments. Crop development is life-cycle progression from seed germination to crop maturity, whose expression is primarily determined by the photo-thermal characteristics of the growth environment as long as enough soil water is available to the crop. Crop growth and economic yield are determined by genetic material, climate, soils and crop management. Plant breeders in the past have continuously modified genetic traits of a crop to breed new varieties to improve productivity and stability of yields in target environments, for example, producing short- or long-duration crop varieties to match the crop duration to water availability periods, increasing biomass productivity and greater partitioning to reproductive organs for higher grain yields or breeding varieties of short stature to minimize lodging as a result of high inputs of fertilizers.

Increased concentration of green house gases (GHGs) in the atmosphere is warming the globe (IPCC 2007). This is causing climate change in terms of increased air temperature and variability in the amount, distribution and intensity of rainfall depending upon the location on the globe. This is gradually changing the agro-climatic characteristics of the environments where food crops are currently grown. With further climate change in future, productivity of crops, especially in tropical regions, may be adversely affected thus threatening food security in these regions; while in other regions, it may improve crop growth conditions for higher productivity. To cope with climate change, we should increase our efforts to breed crop varieties with optimized genetic traits to maintain or improve yields under expected future climate environments.

Plant growth simulation models that integrate various physical and physiological processes of plant growth and development can be used to assess growth and yield of different crop cultivars in different environments by using environment-specific weather, soil and agronomic management data (Boote et al. 2001, 2003). As these models incorporate cultivar-specific parameters that represent genetic traits of cultivars, these can be modified within the observed limits of their genetic variability, and their effects on crop performance can be evaluated singly or in multiple combinations in target environments (Boote et al. 2001). Various parameters and traits that are currently considered crop- or ecotype-specific in the models are also potential targets as genotypic traits to be evaluated. Many researchers in the past have used crop models for proposing plant ideotypes or for genetic improvement of crops for higher yields (Landivar et al. 1983, Boote and Jones 1986, Whisler et al. 1986, Boote and Tollenaar 1994, Hammer et al. 1996, Yin et al. 1999, Boote et al. 2001, 2003, Hammer et al. 2002, 2004, 2005, Tardieu 2003, White and Hoogenboom 2003, Messina et al. 2006, Suriharn et al. 2011). However, most of these efforts have not considered genetic improvement in the context of adaptation of crop plants to climate change. With improved knowledge, understanding and modelling of crop response to climate change factors (high temperatures, increased rainfall variability, increased atmospheric CO_2 concentration and their interactions), crop models have excellent potential to assess genetic improvement of crops to increase yields and optimize adaptation to current and future target environments.

Groundnut (*Arachis hypogaea* L.) is an important oilseed and food crop grown by small and marginal farmers in India in diverse agro-climatic environments. It is grown largely (83 % of total groundnut area) under rainfed conditions during the main rainy season (June/July–October/November) and the remaining 17 % is irrigated mainly in the post-rainy (October–March) season. While India has the largest area under groundnut (6.36 million ha) in the world, its production (6.5 million tons) and productivity have remained low (1022 kg ha^{-1}); the latter being well below the world average (Birthal et al. 2010). In view of increasing population and anticipated climate change, production must increase to meet current and future demand for edible oil and vegetable protein in the country. This may be possible through genetic enhancement and agronomic management of the crop for target environments to increase productivity considering both the current and future climate. This simulation study focused on genetic improvement aspects of the groundnut crop for increasing its productivity in India.

The objectives of this study were as follows: (i) to evaluate genetic traits of groundnut for increasing its productivity in current groundnut growing environments of India and (ii) to evaluate the relative importance of genetic traits for increasing and sustaining productivity in the future climate change scenarios.

Materials and Methods

The crop model

We used the CROPGRO model for groundnut (peanut) coupled with the seasonal analysis programme, which are a part of the DSSAT v4.5 (Hoogenboom et al. 2010), to evaluate the genetic traits of groundnut for target environments. The CROPGRO-Peanut model has a long history of development and improvement starting as PNUTGRO in 1985 (Boote et al. 1986). The model has been evaluated extensively against experimental data on cultivars, sowing densities, drought and sowing dates collected in the USA (Gilbert et al. 2002), India (Singh et al. 1994a,b, Bhatia et al. 2009), Ghana (Naab et al. 2004) and Thailand (Anothai et al. 2009, Putto et al. 2009, Suriharn et al. 2011). It has been used to select best sites for testing breeding lines (Putto et al. 2009), to evaluate multi-environment trials (Anothai et al. 2009), and to determine optimum ideotype (Suriharn et al. 2011). The major components of the groundnut model are vegetative and reproductive development, carbon balance, water balance and nitrogen balance (Boote et al. 1998). It simulates groundnut growth and development using a daily time step from sowing to maturity and ultimately predicts yield. Genotypic differences in growth, development and yield of crop cultivars are affected through genetic coefficients (cultivar-specific parameters) that are input to the model in addition to crop-specific coefficients that are considered less changeable or more conservative in nature across crop cultivars. The physiological processes that are simulated describe crop response to major weather factors, including temperature, precipitation and solar radiation and include the effect of soil characteristics on water availability for crop growth. In the model, high temperature influences growth and development and reduces allocation of assimilates to the reproductive organs through decreased pod set and seed growth rate. The model prediction of elevated temperature effects on pod yield was tested and shown to predict well (Boote et al. 2010) against elevated temperature data (Prasad et al. 2003). Changes in rainfall characteristics influence soil water balance and thus the pattern of water availability to the crop during its life cycle. Increased

CO_2 concentrations in the atmosphere increase crop growth through increased leaf-level photosynthesis, which responds to CO_2 concentration using simplified Rubisco kinetics similar to Farquhar and von Caemmerer (1982). Ability of the CROPGRO model to predict accurate leaf and canopy assimilation response to CO_2 has been shown for soybean (Alagarswamy et al. 2006) and groundnut (Boote, personal communication, 2006). Increased CO_2 concentration reduces transpiration from the crop canopy via an empirical relationship between canopy conductance and CO_2 concentration. Thus, the model has the potential to simulate crop growth and development of groundnut under climate change conditions, such as high air temperatures, variability in rainfall and increased CO_2 concentrations in the atmosphere, and their interaction with genetic traits of the crop that ultimately result in final crop yields at maturity.

Model inputs

The minimum data set required to simulate a crop for a site are described by Jones et al. (2003). Briefly, it includes site characteristics (latitude and elevation), daily weather data (solar radiation, maximum and minimum air temperatures and precipitation), basic soil profile characteristics by layer (saturation limit, drained upper limit and lower limit of water availability, bulk density, organic carbon, pH, root growth factor, runoff and drainage coefficients) and management data (cultivar, sowing date, plant population, row spacing, sowing depth and dates and amounts of irrigation and fertilizers applied). The cultivar data include the genetic coefficients or the cultivar-specific parameters (quantified traits) that distinguish one cultivar from another in terms of phenological development, growth and partitioning to vegetative and reproductive organs and seed quality (Boote et al. 2001).

Determination of genetic coefficients of cultivars

The model requires genetic coefficients for the groundnut cultivars JL 24 (Spanish) and M 335 (Virginia) used in this study for simulating their growth and yield. These cultivars represent farmers' preference to grow Spanish type in southern India and Virginia type in northern and western India. To calibrate and validate the groundnut model for crop development, growth and yield of these varieties, data sets available with ICRISAT for the 1986–1991 seasons and multi-site Initial Variety Trials–II (IVT-II) data obtained from the Annual Reports of the All India Coordinated Research Project on Groundnut (AICRPG 1991–2007) were used. All the available agronomic management data of the IVT-II trials conducted at six contrasting sites for JL 24 and three sites for M 335 were used to prepare the management files (.pnx files) needed to simulate growth and yield of groundnut. Crop data available from these trials were days to physiological maturity, final plant stand, pod and seed yields, 100-seed weight and shelling percentage. The weather and soils data of the trial sites were also input to the files needed for model execution. ICRISAT crop data sets (ICRISAT Patancheru and Coimbatore sites data for cv. JL 24 and Ludhiana site data for cv. M 335) included periodic observations on crop phenology, crop growth and yields at harvest. First, the two cultivars were calibrated for their genetic coefficients against the ICRISAT data sets, and later these coefficients were further refined with minor changes, especially for crop life cycle, using 30 % of data sets of the IVT-II trial sites. The remaining data sets were used for model validation. As complete information on agronomic management and crop growth was not available for the IVT-II trials, we compared only the maximum, minimum and mean pod yields simulated by the model over the years with the reported maximum, minimum and mean pod yields for the sites to evaluate model performance. We assumed that the maximum yields were obtained without any major abiotic or biotic constraints, while minimum yields were obtained under the overriding impact of drought over other types of stresses.

The study sites and the input data

Simulations of climate change impacts and genetic traits evaluation were carried out for six sites (Jaipur and Junagadh for cv. M 335; Anantapur, Dharwad, Belgaum and Coimbatore for cv. JL 24) representing a broad range of agro-climatic conditions experienced by the groundnut crop. These sites include the major groundnut growing areas (Anantapur and Junagadh) of India. Jaipur and Junagadh sites are warmer with sufficient water availability during the cropping period. Anantapur and Coimbatore sites are warmer but have low water availability, either because of low rainfall or because of low water-holding capacity of soil. Dharwad and Belgaum are cooler sites with sufficient water availability. The geographical and soil characteristics of the sites are given in Table 1, whereas the baseline climatic characteristics and the projected changes in climate for the sites are given in Table 2. Long-term records of weather data for the sites were obtained from the India Meteorological Department (IMD), Pune and Agricultural Research Institutes in India. For most sites, only daily rainfall and maximum and minimum temperature data were available. Solar radiation for the sites was estimated from the temperature data following the method of Bristow and Campbell (1984). The soil profile data for the target sites were obtained from soil survey bulletins published by the National Bureau of Soil Survey and Land Use Planning, Nagpur, India (Lal et al. 1994 and Reddy et al. 2005). Soil parameters were estimated from the soil survey data using

Table 1 Geographical and soil characteristics of the target sites

	Jaipur	Junagadh	Anantapur	Coimbatore	Dharwad	Belgaum
Latitude (°)	26.92	21.31	14.68	11.00	15.43	15.8
Longitude (°)	75.82	70.36	77.62	76.97	75.12	74.5
Elevation (m)	100	228	420	39	675	753
Soil type	Entisol	Inceptisol	Alfisol	Inceptisol	Vertisol	Alfisol
Soil depth (cm)	170	165	90	124	195	176
EWHC (mm)1	155	200	78	200	210	200

[1]Extractable water-holding capacity of soil.

Table 2 Baseline (Base) and projected (Proj) increase in maximum and minimum monthly temperatures and percentage change in monthly rainfall by 2050 at the target sites as per the UKMO-HADCM3 GCM model for the SRES A1B scenario

	Jaipur		Junagadh		Anantapur		Coimbatore		Dharwad		Belgaum	
Month	Base	Proj	Base	Proj	Base	Proj	Base	Proj	Base	Proj	Base	Proj
	Maximum temperature (°C)											
June	39.6	1.6	35.3	1.8	35.4	1.9	32.1	2.4	30.4	2.4	29.4	2.0
July	34.6	0.3	31.8	0.9	33.5	2.1	31.2	2.8	28.6	2.5	26.7	2.1
August	33.0	0.0	30.7	0.2	32.7	1.8	31.6	2.9	28.4	2.0	26.3	1.6
September	34.4	1.2	32.8	1.0	32.6	2.1	32.3	3.0	29.7	2.6	28.2	2.2
October	34.0	1.1	35.7	0.9	32.0	2.6	31.5	2.7	30.3	3.1	29.8	2.7
Mean maximum	35.1		33.3		33.2		31.7		29.5		28.1	
	Minimum temperature (°C)											
June	27.4	2.6	27.1	2.5	24.4	2.6	22.5	2.7	21.6	2.9	21.4	2.6
July	25.8	1.7	25.8	2.0	23.7	2.4	22.0	2.5	21.2	2.5	20.8	2.1
August	24.8	1.9	25.0	1.8	23.3	2.0	22.0	2.4	20.8	1.9	20.4	1.7
September	23.6	3.4	24.0	2.9	23.0	2.4	22.1	2.6	20.6	2.6	19.8	2.2
October	19.7	3.0	21.6	2.7	22.0	3.2	22.0	2.9	20.5	3.3	19.1	3.0
Mean minimum	24.3		24.7		23.3		22.1		21.0		20.3	
Mean temperature	29.7		29.0		28.3		26.9		25.2		24.2	
	Rainfall (mm) and % change											
June	53	−33	99	−50	55	−13	29	−92	78	−55	132	−37
July	183	66	327	19	74	−16	35	−64	67	−9	193	5
August	176	55	148	55	87	−3	29	−71	79	−3	179	9
September	58	84	67	54	140	−1	51	−9	99	7	124	13
October	29	50	43	45	99	−13	141	−17	92	−11	85	−9
Total	500		684		455		284		415		712	

the SBuild program available in DSSAT v4.5 (Hoogenboom et al. 2010).

Projected climate change at the target sites

Simulation of climate change impacts required projected climate change data to modify the observed weather data of sites. Statistically downscaled (delta method) projected climate data for the 2050 time slice with 2.5 arc-min resolution (5 km^2 resolution) and the WorldClim baseline (1960 –1990) climate data with 30 arc-s resolution (1 km^2 resolution) were downloaded for the six target sites from CIAT's climate change portal (http:/ccafs-climate.org//download_sres.html#down). The projected climate data comprised of monthly values of maximum and minimum temperatures and rainfall predicted by the UKMO-HADCM3 GCM model for the SRES A1B scenario. The difference between projected monthly maximum and minimum temperatures by 2050 compared to baseline values gave the delta changes in temperature. The percentage deviations in monthly rainfall by 2050 from the baseline values were also calculated (Table 2).

Monthly changes in maximum and minimum temperature and rainfall along with CO_2 increase as per the ISAM model (IPCC 2001) were input to the 'environmental modifications section' of the management files of the crop model (.PNX). Temperatures were entered as change in temperature (delta values), rainfall as ratio of projected rainfall to baseline rainfall and CO_2 as absolute value against first day of each month. These climate change values modify the observed baseline weather data of a given month until it reads the new set of values for the next month. As the rainfall was entered as ratio, it affected the value of each rainfall event rather than altering the pattern of rainfall distribution. The time period of the observed baseline weather data used for simulation was 1973–2002 for Anantapur, 1975–2002 for Belgaum, 1973–2002 for Coimbatore, 1973–2002 for Dharwad, 1973–2002 for Jaipur, and 1985–2006 for Junagadh. The observed baseline data correspond to the WorldClim baseline data.

Climate change scenarios and model evaluation of plant traits

The effect of modifying plant traits (genetic coefficients) on crop yield was simulated with and without climate change, that is, with and without modifying the baseline weather data, along with the projected changes in CO_2 concentration in the atmosphere. It is estimated that by 2050, the atmospheric CO_2 concentration will increase to 530 ppm (IPCC 2001) from the current level of 380 ppm. The following four treatments consisting of baseline climate and future climate change scenarios (changes in temperature, CO_2 and rainfall) were considered for each target site to evaluate the genetic traits of groundnut:

1 Simulation with baseline climate
2 Simulation with projected increase in maximum and minimum temperatures by 2050
3 Simulation with projected increase in maximum and minimum temperatures and 530 ppm CO_2 concentration of the atmosphere and
4 Simulation with projected increase in maximum and minimum temperatures, 530 ppm CO_2 and projected change in rainfall.

For each site, the simulations were initiated on 15 May each year, and the soil profile was considered to be at the lower limit (SLL) of water availability on that day. Considering the spatial and temporal variations in the onset of rainy season and actual farmers' practice, the sowing window assumed was 1 June to 15 August each year for the target sites, except for Anantapur where the sowing window was taken as 20 June to 15 August. The simulated crop was sown on the day when soil moisture content in the top 30-cm soil depth had reached at least 40 % of the extractable water-holding capacity during the sowing window. A plant population of 25 plants m^{-2} and row spacing of 30 cm were considered for simulating groundnut growth. Soil-limited photosynthesis factor (SLPF) value of 0.74 was used for Anantapur, 0.90 for Belgaum, 0.92 for Coimbatore, 0.97 for Dharwad, 0.90 for Jaipur and 0.95 for Junagadh. Site-specific values of SLPF were calibrated such that a single value of light-saturated leaf photosynthesis (AMAX) from literature accurately predicted biomass and yield over all sites. An SLPF value <0.90 represents soil limitations beyond N or water.

For evaluating plant traits, sensitivity analysis was carried out by changing selected genetic coefficients of groundnut cultivars JL 24 and M 335 and crop parameters from the species file (PNGRO045.SPE) of the groundnut model. These coefficients/parameters (representing plant traits) affect crop development cycle, growth and partitioning of assimilates to vegetative and reproductive organs and, therefore, the yield of groundnut in a given agro-climatic and management environment. The selected plant traits and changes made in their parameter values for sensitivity analysis are given below. The use of 10 % change in a parameter is common in sensitivity analyses, but in this case, 10 % change is rather conservative in relation to the feasible genetic range.

Phenological traits
Emergence to beginning of flowering duration (EM-FL) increased by 10 %, beginning seed-fill to physiological maturity duration (SD-PM) increased by 10 %, EM-FL and SD-PM both increased by 10 %, and SD-PM increased by 10 % but EM-FL reduced to keep the maturity duration same.

Crop growth traits
Maximum leaf photosynthesis rate (AMAX), specific leaf area (SLA) and leaf size (SIZLF) were each increased by 10 %. Nitrogen mobilization from the leaves (NMOB) was decreased by 10 %.

Reproductive traits
Pod adding duration (PODUR) was decreased by 10 % to make the cultivar more determinant. Seed-filling duration (SFDUR) and the coefficient for maximum partitioning to pods (XFRT) were each increased by 10 %.

Root traits
Assimilate partitioning to roots increased by 2 % (percentage units) by reducing partitioning to leaves and stems, rate of rooting depth increase (RTFAC) was increased by 10 %; relative distribution of roots in the soil profile (SRGF) was decreased by 10 % for top 30-cm soil zone but increased by 10 % below 30-cm, turgor-induced shift of partitioning from shoot to root (ATOP) decreased from 0.80 to 0.0 (no shift) to make root growth less adaptive to plant water deficit. ATOP of 1.0 represents maximum adaptive shift in partitioning to root.

Temperature tolerance
Temperature tolerance (TT) of pod set, partitioning to pods, and single seed growth rate were each increased by 2 °C.

Combination of traits
Various combinations of genetic traits, such as AMAX and TT with crop phenology, growth and partitioning traits, were also attempted to evaluate the degree of additivity of promising traits for pod yield enhancement at each site.

The impact of climate change scenarios on phenology, yield and yield components of groundnut crop was assessed relative to their respective mean values simulated for the baseline climate of the sites. The effect of changes in plant traits on pod yield of groundnut was assessed by comparison with the mean pod yield simulated for the standard default cultivar in the respective climate scenarios of the sites.

Results

Regression of simulated pod yields of the two cultivars against observed data of the test sites showed a strong relationship between simulated and observed yields (cv. JL 24: $Y = 1.036X - 193.0$, $R^2 = 0.90$; and cv. M 335: $Y = 0.929X + 259.6$, $R^2 = 0.82$) (Fig. 1). The d-value, a measure of model predictability (Willmott, 1982), was also high for the cultivars (0.97 for JL 24 and 0.92 for M 335). These results confirm that the genetic coefficients of the two cultivars are accurate and that the CROPGRO model can be reliably used to simulate the growth and yield of groundnut for different soil-climate environments of India. The estimated genetic coefficients for the two cultivars are presented in Table 3. The intention of model calibration was to set the baseline cultivar as a starting point for genetic sensitivity.

Impact of climate scenarios on phenology, yield and yield components

As CO_2 and rainfall do not affect crop development, only the effect of temperature on phenology of groundnut has been considered here. Crop season mean temperature of the sites ranges from 24.2 to 29.7 °C (Table 2). Increase in temperature hastened flowering and crop maturity at sites where mean temperatures during the cropping period were <28 °C (Table 4), but once the mean temperature of the sites exceeded this value, the crop development was delayed. The magnitude of delay or hastening of crop development depended upon the current value of seasonal mean temperatures at a site and the future scenario of temperature increase. At Jaipur, Junagadh and Anantapur where the current mean temperatures exceed 28 °C, the flowering and physiological maturity were delayed up to 3 days with the increase in temperature. At Dharwad and Belgaum, physiological maturity was hastened by 4 days with the increase in temperature (Table 4).

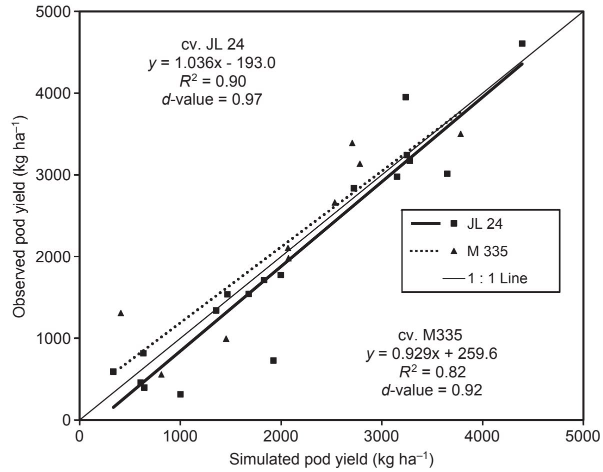

Fig. 1 Relationship of simulated pod yield of the two cultivars with the observed yield across locations of India.

Pod yield across locations ranged from 1000 to 3370 kg ha^{-1} in the baseline climate depending upon agro-climatic conditions of the sites and the cultivar grown (Table 4). Higher mean yields were obtained at cooler sites of Dharwad (2960 kg ha^{-1}) and Belgaum (3370 kg ha^{-1}) where water availability to the crop was also sufficient for crop growth. This was followed by warmer sites with sufficient water availability (Jaipur and Junagadh) where mean pod yields ranged from 2210 to 2230 kg ha^{-1}. At warmer sites with less water availability (Anantapur and Coimbatore), the mean pod yields ranged from 1000 to 1820 kg ha^{-1}. Increase in temperature by 2050 decreased pod yield at all the sites. The magnitude of decrease depended upon the baseline climate, the projected increase in temperature and the water-holding capacity of soils at the sites. The maximum decrease in yield was at Coimbatore (33 %) and the minimum at Belgaum (11 %) with the increase in temperature. Increase in CO_2 increased the yield by 14–20 % across sites, but the yields at Jaipur, Anantapur and Coimbatore were still 2–19 % below the yields simulated with baseline climate. In the temperature + CO_2 + rainfall scenario, simulated mean pod yield for the sites depended upon the projected changes in rainfall for the sites; the model simulated maximum gain of 19 % at Jaipur and a maximum loss of 44 % at Coimbatore. For a given cultivar, pod yields simulated for the sites were related to the number of pods per plant and the seed size; as the number of seeds per pod mostly remained the same across sites and climate scenarios (data not shown). Increase in temperature associated with climate scenarios reduced the number of pods per plant and seed size at all the sites (Table 4). Temperature + CO_2 scenario increased the number of pods per plant with better plant growth, whereas the temperature +

Table 3 Genetic coefficients (GC) of JL 24 (Spanish) and M 335 (Virginia) used for simulation

GC name	Genetic coefficient definition	JL 24	M 335
CSDL	Critical short day length below which reproductive development progresses rapidly with no day length effect (h)	11.84	11.84
PPSEN	Slope of the relative response of development to photoperiod with time (1 per h)	0.0	0.0
EM-FL	Time from emergence to first flower appearance (ptd)	17.4	20.0
FL-SH	Time from first flower to beginning of pod growth (ptd)	7.0	8.0
FL-SD	Time from first flower to beginning of seed growth (ptd)	17.5	20.3
SD-PM	Time from beginning of seed growth to physiological maturity (ptd)	62.0	70.0
FL-VS	Time from first flower to last leaf on main axis (ptd)	70.0	68.0
FL-LF	Time from first flower to end of leaf expansion (ptd)	70.0	78.0
LFMAX	Maximum leaf photosynthetic rate at 30°C, 350 ppm CO_2, and high light (mg CO_2 m^2 s^{-1})	1.36	1.36
SLAVR	Specific leaf area of cultivar under standard growth conditions (cm^2 g^{-1})	245.0	270.0
SIZLF	Maximum size of full leaf (compound leaf) ($cm^{2)}$	16.0	18.0
XFRT	Maximum fraction of daily growth partitioned to seed + shell	0.84	0.85
WTPSD	Genetic potential weight per seed (g)	0.55	0.90
SFDUR	Seed-filling duration for pod cohort (ptd)	28.0	30.0
SDPDV	Seeds per pod at standard growth conditions (# pod^{-1})	1.65	1.65
PODUR	Duration of pod addition (ptd)	15.0	22.0
THRSH	Threshing (Shelling) percentage, maximum % of seed to seed + shell	78.0	75.0
SDPRO	Potential seed protein (fraction)	0.27	0.27
SDLIP	Potential seed lipid (fraction)	0.51	0.51

ptd, photothermal days.

Table 4 Effect of climate scenarios on phenology, yield and yield components of groundnut at the six sites

Climate scenario	Jaipur	Junagadh	Anantapur	Coimbatore	Dharwad	Belgaum
			Days to 50 % flowering1			
Baseline	30	28	26	26	26	27
Temperature	31	29	27	26	26	27
			Days to physiological maturity1			
Baseline	124	121	107	104	109	113
Temperature	125	121	110	104	105	109
			Pod yield (kg ha^{-1})			
Baseline	2210	2230	1000	1820	2960	3370
			Percentage change in pod yield from baseline			
Temperature	−20	−18	−18	−33	−19	−11
Temperature + CO_2	−5	1	−2	−19	1	7
Temperature + CO_2 + rain	19	9	−6	−44	−10	6
			Number of pods per plant			
Baseline	12	11	9	19	22	25
Temperature	10	9	8	14	20	25
Temperature + CO_2	12	12	10	17	25	30
Temperature + CO_2 + rain	14	12	10	12	23	30
			Seed weight (g $seed^{-1}$)			
Baseline	0.47	0.57	0.29	0.27	0.41	0.43
Temperature	0.42	0.52	0.26	0.24	0.36	0.37
Temperature + CO_2	0.42	0.53	0.26	0.24	0.36	0.38
Temperature + CO_2 + rain	0.47	0.53	0.25	0.23	0.35	0.37

[1]In the CROPGRO model for groundnut, the phenology is determined primarily by temperature.

CO_2 + rainfall scenario increased or decreased the number of pods per plant depending upon the projected changes in rainfall for the sites. Changes in CO_2 and rainfall had marginal effects on seed size across sites.

Yield response to phenology traits

Pod yield response to changes in duration of various growth cycle phases was influenced by the cultivar grown, the baseline climate and the future climate change scenarios of the sites. Increasing the duration of emergence to flowering (EM-FL) by 10 % either had a negative or had no effect on pod yield at warmer sites with all the climate change scenarios. However, a marginal yield gain to the extent of 1.8 % was simulated for the cooler sites of Dharwad and Belgaum (Fig. 2a). Increasing the duration of beginning seed-fill to physiological maturity (SD-PM) by 10 % enhanced pod yield at all sites to varying degree. At Jaipur and Junagadh for cv. M 335, increasing the duration of SD-PM phase increased pod yields by 0.5–2.0 % with baseline and future climate scenarios (Fig. 2b). The maximum increase in pod yield was obtained at Anantapur by increasing SD-PM, followed by Coimbatore, Dharwad and Belgaum. Increasing the duration of both EM-FL and SD-PM by 10 % did not increase the pod yields at warmer sites (Jaipur, Junagadh and Coimbatore), except at Anantapur where 6.9–9.3 % increase in pod yield was simulated across climate scenarios (Fig. 2c). This is mainly attributed to the relatively longer period of rainfall at this site, in spite of being low rainfall and warm site. At cooler sites with sufficient water availability during the season (Dharwad and Belgaum), pod yields increased by 3.2–5.0 % across climate scenarios. When SD-PM was increased by 10 % without changing the maturity of the crop, pod yields increased at the warmer sites, but decreased at the cooler sites with all climate scenarios (Fig. 2d). Higher benefits up to 9.4 % increase in pod yield were simulated for Jaipur, Junagadh and Anantapur than at Coimbatore. These results indicate that in both baseline and future climate scenarios, the pod yields can be increased by increasing the duration of both EM-FL and SD-PM phases at cooler sites, whereas, at warmer sites, pod yields can be increased by increasing the duration of SD-PM without changing the time to crop maturity.

Yield response to growth traits

Among the crop growth traits, increasing the rate of maximum leaf photosynthesis (AMAX) consistently contributed to increase in pod yield across sites and climate scenarios (Fig. 3a). When AMAX was increased by 10 %, pod yields increased by 3.1–4.8 % across sites with greater increase at cooler sites (Dharwad and Belgaum) or warmer sites with sufficient water availability (Junagadh). Second in importance for consistent yield increase was decreasing nitrogen mobilization from leaves (NMOB) for all sites and climate scenarios (Fig. 3d). When NMOB was decreased by 10 %, benefit to pod yield ranging from 1.6 to 2.4 % was simulated for the warmer sites, except Coimbatore, for the climate scenarios, whereas the yield increase for this plant trait at cooler sites was somewhat less. Small but consistent increase in pod yield for 10 % increase in both specific leaf area (SLA) and leaf size (SIZLF) was simulated at cooler sites (Fig. 3b, c). Increasing the magnitude of these two traits was not beneficial for the warmer sites and the yields substantially reduced at the Coimbatore site.

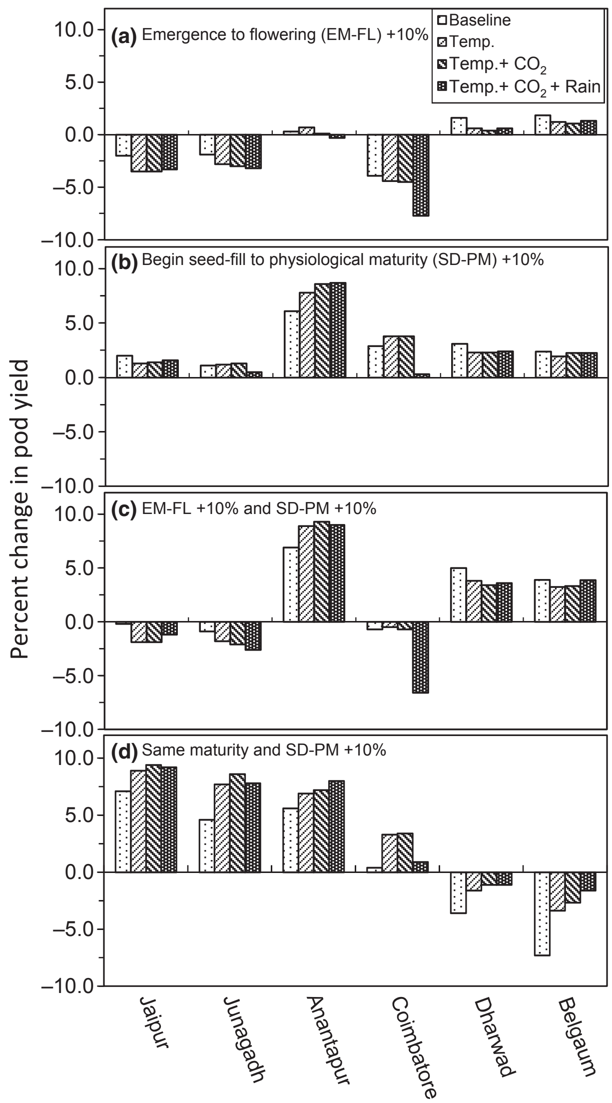

Fig. 2 Percentage change in pod yield with change in phenology traits relative to the mean yield simulated for baseline and climate scenarios for the six sites.

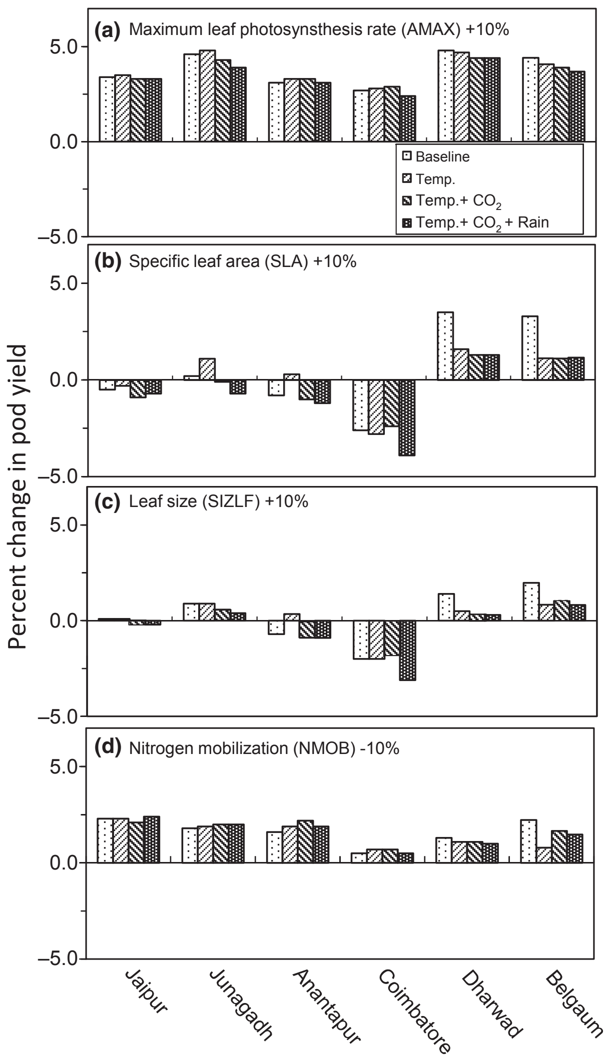

Fig. 3 Percentage change in pod yield with change in growth traits relative to the mean yield simulated for baseline and climate scenarios for the six sites.

Yield response to reproductive traits and TT

Decreasing pod adding duration by 10 % increased pod yield at the warmer sites and decreased yield at cooler sites (Fig. 4a). Pod yield increase with decreasing PODUR was higher at Jaipur (4.3–5.7 %) than at Junagadh (0.6–2.8 %) regardless of the climate scenarios. This is attributed to relatively less rainfall at Jaipur than at Junagadh during the crop season, indicating the need for more determinate type (faster pod adding rate) for higher yields at Jaipur in both the baseline and future climates. Coimbatore being a low rainfall site also showed greater positive response to this trait compared with Anantapur. Increasing seed-filling duration (SFDUR) and maximum partitioning to pods (XFRT) each by 10 % consistently increased pod yield at all the sites and climate scenarios; however, the responses were larger for XFRT than for SFDUR (Fig. 4b, c). The benefit of XFRT was enhanced at elevated temperature and CO_2 associated with climate change scenarios, whereas such effect was not present for SFDUR. Increasing TT of pod addition and seed growth by 2 °C increased pod yield at warmer sites and had negligible effect at the cooler sites (Fig. 4d). The contribution of this trait to pod yield increased with the increase in temperature, especially at warm sites. The increase in pod yield ranged from 7.0 to 12.5 % at Jaipur and 2.6 to 10.3 % at Coimbatore for various climate scenarios, while at other two sites, it was limited to 4.5 %. These results show that the relative effect of TT on pod yield will be more at warmer sites and warmer climate scenarios.

Yield response to root traits

Increased partitioning to roots decreased pod yield at most sites with larger decrease in more favourable temperature and water availability environments (Fig. 5a). The beneficial effects of increasing the rate of rooting depth or increasing relative root distribution (SRGF) in soil profile below 30-cm depth were greater at sites where water availability to the crop was high either because of high rainfall (Junagdh and Belgaum) or because of deeper soil (Dharwad) (Fig. 5b, c). However, between these two traits, the benefits were larger for SRGF. When the turgor-induced shift of partitioning to roots (ATOP) was eliminated (set to zero) in the model, the pod yield decreased to varying degrees at all target sites and climate scenarios (Fig. 5d). Greater effect on pod yield because of this trait was simulated for the sites where soils are deep (Junagadh, Dharwad and Coimbatore) as compared to other sites. At Belgaum, where rainfall is the highest among the target sites and the temperatures are the lowest, the effect on pod yield was negligible. These results show that turgor-induced shift in partitioning to roots is an important trait for providing drought resistance to the groundnut crop and its benefits are greater especially on deeper soils having high water-holding capacity.

Yield response to the combination of traits

The effect of combination of promising traits on pod yield of groundnut was evaluated for three sites: Junagadh (warm with sufficient water availability), Anantapur (warm with low water availability) and Belgaum (cool with sufficient water availability). In general, when promising traits were evaluated in increasing number of combinations, the pod yields progressively increased at all three sites (Table 5). At Junagarh, when AMAX, SD-PM, SFDUR,

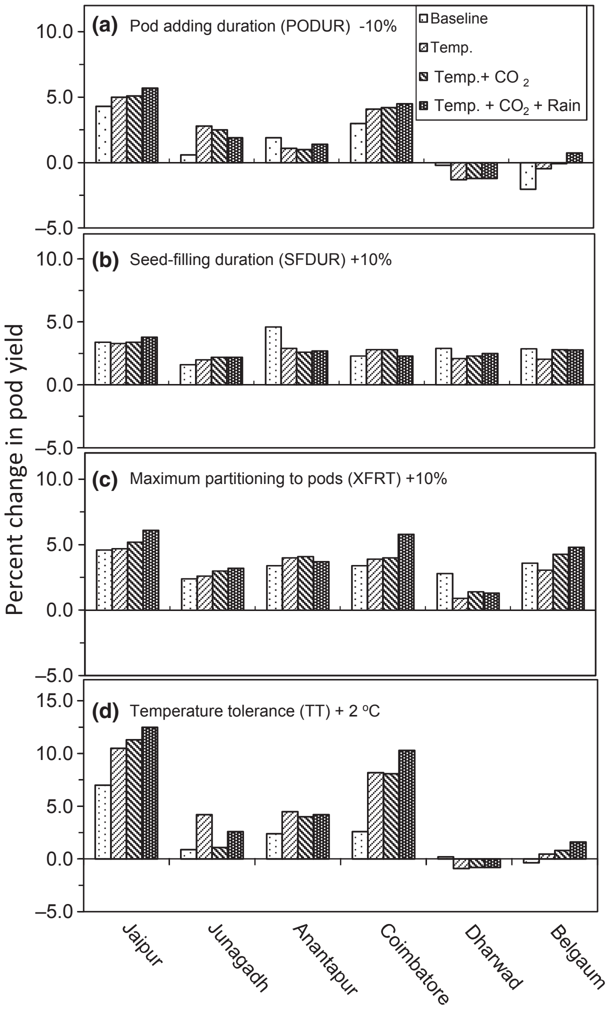

Fig. 4 Percentage change in pod yield with change in reproductive and temperature tolerance traits relative to the mean yield simulated for baseline and climate scenarios for the six sites.

XFRT, PODUR and TT traits were combined, the pod yield increased by 12.1–17.2 % across climate scenarios. Because of projected increased in rainfall at this site in future, the benefit of combining traits decreased to 14.7 % for the temperature + CO_2 + rainfall scenario. For the Anantapur site, the combination of AMAX, SD-PM, SFDUR, XFRT, PODUR and TT traits increased the pod yield by 22.9–29.2 % across climate scenarios. Contribution of the TT trait in combination with other traits was greater at this site than that simulated for Junagadh. At Belgaum, inclusion of TT in the trait combinations did not increase pod yields. These results indicate that the effect of individual plant traits, whether positive or negative on pod yield, are usually expressed when evaluated in combinations and, therefore, their combined effect is additive on pod yield.

Discussion

Climatic effects on yield

Effects of climate change compared to baseline can be analysed from their respective contributing components, with yields being decreased at all sites with warming alone, being increased sufficiently by elevated CO_2 that yields were mostly recovered to baseline at the temperature-plus-CO_2 case, and being decreased or increased for the case of temperature-plus-CO_2-plus rainfall. For India, the climate change scenarios feature increased rainfall at some sites, but less at other sites (Anantapur and Coimbatore, for example, had less yield for this scenario). Changes in pod yield with increase in temperature at all sites were influenced by change in the duration of growth cycle phases, decrease in the number of pods per plant and seed size. Crop maturity was hastened at a site where the mean temperature during cropping season was <28 °C and delayed where it was more than this threshold value. Challinor et al. (2007) using GLAM model also reported increase in duration of groundnut crop for the regions in India where the mean temperatures with climate change scenario exceeded the optimum temperature (28 °C) required for crop development. The simulated effects on yield components of groundnut are also consistent with the results obtained by Prasad et al. (2003) in a controlled-environment growth study in which decrease in pod yield of groundnut was associated with decrease in number of pods per plant, number of seeds per pod and seed size with increasing temperature. Increase in CO_2 had beneficial effect on yield and yield components. Thus, for the future climates of increasing temperatures and varying duration of water availability at the target sites, shorter or longer duration cultivars having capability to set more pods per plant with larger seed size at high temperatures will be needed.

Genetic trait effects and interaction with environment

The general case for the genetic traits will be discussed in an explanatory manner to illustrate the mechanism for response. Generally, increasing the time to flowering (EM-FL) serves to increase leaf area index, thus improving light interception and photosynthesis, allowing higher yield if the season length is not compromised by terminal water deficit. This trait had relatively minor effects at most sites, except at the drought-prone Coimbatore site where the higher LAI (from later flowering or higher SLA or greater leaf size) apparently enhanced the water-stress. Longer time from beginning seed to physiological maturity (SD-PM) in the model usually is a yield-enhancing trait as it increases the time for photoassimilation and allocation of assimilates

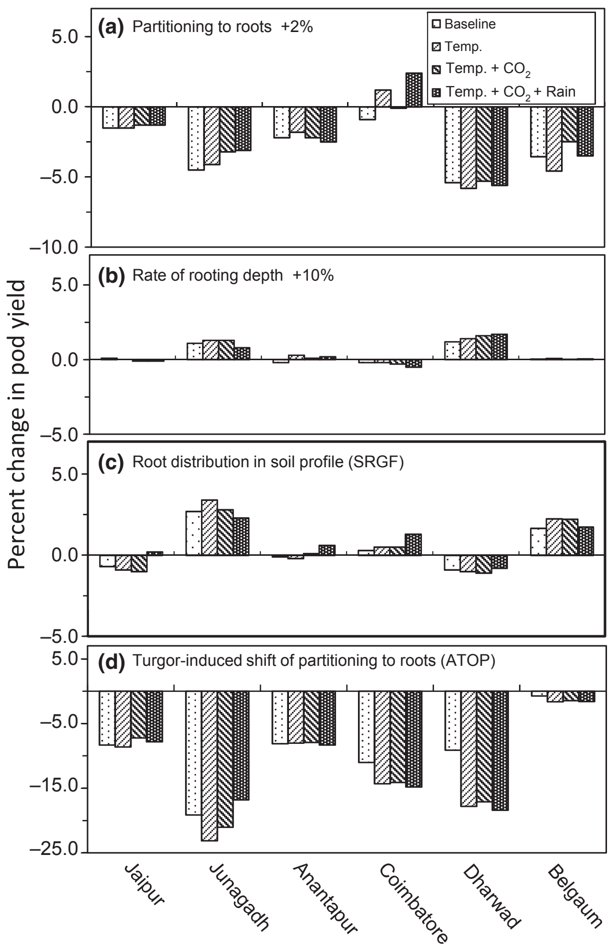

Fig. 5 Percentage change in pod yield with change in root traits relative to the mean yield simulated for baseline and climate scenarios for the six sites.

to pods. Yield increases from 10 % longer SD-PM ranged from 1.1 to 6.1 % for baseline weather, being greatest at Anantapur, particularly under altered climate. Anantapur may benefit from late-extended but sporadic monsoon. Increasing both time to flower and seed to physiological maturity generally gives a greater enhancement of yield than either trait alone, especially at Anantapur; however, at Coimbatore, the negative effect of longer time to flower dominated to create a negative effect. Where season length does not allow or growers insist on early maturity, same life cycle can be achieved by longer time from seed to physiological maturity, but shorter time to flower. This case was beneficial to yield at Jaipur, Jungadh and Anantapur, but was not beneficial at other (especially cooler) sites as the crop would have a lower leaf area index for the same life cycle.

Photosynthesis traits were anticipated to be positive, based on the way the crop model functions. In this case, 10 % higher leaf photosynthesis resulted in 2.7–4.8 % yield increase for baseline weather at the various sites. Less than proportional yield increase was expected, because single leaf photosynthesis only gives a 3–4 % simulated increase in canopy assimilation as discussed by Boote et al. (2003). The photosynthesis trait did not show up differentially in the climate scenarios. Increased specific leaf area (SLA) has the effect of increasing leaf area index for the same amount of leaf mass and causes increased canopy assimilation. This trait was beneficial in some environments (Dharwad, Belgaum) where the temperatures are currently cooler, negative in some (drought-prone Coimbatore) and negligible in others. Increasing leaf size (SIZLF is a stand-in for early leaf growth vigour) was similar acting to SLA, having beneficial effects at Dharwad and Belgaum, but negative effects at Coimbatore. Again, the probable mechanism is that the increased leaf area from either of these causes more drought stress that reduces yield. Slower leaf N mobilization (similar to stay-green) should give more sustained canopy assimilation during the seed-filling phase and was expected to increase yield. This trait had modest benefits of 0.5–2.3 % increase in yield.

Reproductive traits included a more determinant pod addition (shorter PODUR), which had small benefits in some environments, but had negative effects in two cooler environments (Dharwad and Belgaum). Longer single seed growth (SFDUR) is not the same as a longer time from beginning seed to maturity, but rather defines growth duration for single seeds, and with same seed size determines a (slower) single seed growth rate. This trait was generally yield-enhancing (1.6–4.6 %) at all sites and climate scenarios, as it allowed more seeds to be carried for a longer time. The model is not particularly sensitive to potential seed size (WTPSD), giving only small effects (data not shown). Increased partitioning to pods (XFRT) has previously been shown to be a major contributor to groundnut yield improvement (Duncan et al. 1978), and the simulations showed that a 10 % increase (in XFRT value) increased yield 2.4–4.6 % with some beneficial effect under climate change scenarios at Jaipur and Coimbatore. Enhanced TT of pod addition and partitioning was evaluated by shifting the upper failure point up by 2 °C (genetic variation to an extent believed to exist in groundnut). This trait had major effects (7.0 and 2.6 %) in warm environments such as Jaipur and Coimbatore and increased further (10.5 and 8.2 %) under higher temperature climate scenarios at Jaipur and Coimbatore. But it had negligible effects at cool sites such as Belgaum and Dharwad. It is interpreted from these results that incorporation of TT trait in groundnut will increase pod yields up to 10 % in already warm sites, especially in years with low rainfall.

Rooting traits showed an important distinction between constitutive (all the time) partitioning to roots vs. adaptive

Table 5 Effect of trait combinations on percentage change in pod yield of groundnut simulated for baseline and climate scenarios for the three sites

Trait combination	Baseline	Temp.	Temp + CO_2	Temp + CO_2 + Rain
	Junagadh			
Yield without trait modification (kg ha^{-1})	2230	1830	2260	2430
	Percentage increase in pod yield			
AMAX	4.6	4.8	4.3	3.9
AMAX, SD-PM	5.5	6.0	5.6	4.4
AMAX, SD-PM, SFDUR	6.7	8.3	8.0	7.0
AMAX, SD-PM, SFDUR, XFRT	9.6	11.1	11.2	10.6
AMAX, SD-PM, SFDUR, XFRT, PODUR	10.4	13.8	14.0	12.4
AMAX, SD-PM, SFDUR, XFRT, NMOB	11.0	12.8	14.4	12.4
AMAX, SD-PM, SFDUR, XFRT, TT	10.8	15.2	15.6	13.5
AMAX, SD-PM, SFDUR, XFRT, PODUR,TT	12.1	17.0	17.2	14.7
	Anantapur			
Yield without trait modification (kg ha^{-1})	1000	830	990	950
	Percentage increase in pod yield			
AMAX	3.1	3.3	3.3	3.1
AMAX, SD-PM	9.4	11.7	12.3	12.2
AMAX, SD-PM, SFDUR	14.5	15.1	15.1	15.1
AMAX, SD-PM, SFDUR, XFRT	18.2	19.1	19.6	19.2
AMAX, SD-PM, SFDUR, XFRT, PODUR	20.1	21.0	21.5	21.4
AMAX, SD-PM, SFDUR, XFRT, NMOB	20.4	21.8	22.0	21.8
AMAX, SD-PM, SFDUR, XFRT, TT	20.7	25.1	25.6	25.5
AMAX, SD-PM, SFDUR, XFRT, PODUR,TT	22.9	28.4	29.2	29.0
	Belgaum			
Yield without trait modification (kg ha^{-1})	3370	3020	3620	3570
	Percentage increase in pod yield			
AMAX	4.4	4.1	3.9	3.7
AMAX, SD-PM	6.8	6.2	6.3	6.1
AMAX, SD-PM, SFDUR	9.1	8.3	8.7	8.9
AMAX, SD-PM, SFDUR, XFRT	13.5	12.7	13.6	14.2
AMAX, SD-PM, SFDUR, XFRT, PODUR	12.3	13.3	13.8	14.3
AMAX, SD-PM, SFDUR, XFRT, NMOB	15.9	14.9	15.4	15.4
AMAX, SD-PM, SFDUR, XFRT, TT	13.8	14.2	14.7	15.6
AMAX, SD-PM, SFDUR, XFRT, PODUR,TT	12.3	14.4	15.7	16.0

AMAX, maximum leaf photosynthesis rate; SD-PM, beginning seed-fill to physiological maturity; SFDUR, seed-filling duration; XFRT, coefficient for maximum partitioning to pods; PODUR, pod adding duration; NMOB, nitrogen mobilization from leaves; and TT, temperature tolerance.

partitioning to roots. The case of always partitioning more to roots (2 % units more) resulted in less leaf area growth, less photoassimilation, and 0.9–5.4 % less yield. The drought-prone Coimbatore site was the only site to show beneficial effects of the constitutive trait and only in high temperature climate scenarios. By contrast, the ability to shift assimilate to roots only when water-stress occurs (ATOP above 0.0) seems to be a good adaptive feature. The model already has this feature with a value of 0.8, and reducing the value from present 0.8 to 0.0 (no shift) causes major yield reductions approaching 11–19 %, especially at Coimbatore and Junagardh and greater under elevated temperature (related to higher transpiration). The other rooting traits behaved mostly as expected, with small to 2.7 % yield increases from the following: increasing rate of root depth increase and making the root length distribution greater below 30 cm.

In reality, plant breeders often combine multiple traits to create an improved cultivar. Thus, the point of trait combinations was to explore the degree of additivity or interactivity of these various traits in different environments (sites and climates) and to suggest the extent of yield improvement feasible if multiple traits could be combined. The traits were found to be mostly additive and combinations of five or so traits could give yield increases of 10–20 % depending on the site and climate. Successive two-, three- and four-way combinations of traits showed the additivity associated with each new trait. Furthermore, the effects of some traits such as increased thermo-tolerance of reproductive showed to be most beneficial in the high temperature sites and future warm climate.

The simulation results of climate change impacts and evaluation of single or multiple traits are realistic in the sense that crop model employed is mechanistic in terms of simulating the physical and physiological processes of groundnut crop determining its growth and yield under field situations. The plant traits evaluated had both direct and interactive effect on growth and development of the crop leading to final yield at harvest. The yield benefits simulated were prescribed by the extent of trait modifications (usually 10 %) considered in this study; however, the benefits could be even more or less depending upon the true range of variability in traits available in the genetic resources of this crop. We believe that 10 % variation of traits is an underestimate for the tested life-cycle phase durations but could be an overestimation of trait variation for AMAX and SLA. So, it is important to characterize genetic variability for these traits. The additivity of effects of multiple traits is considered reasonable based on our experience in modelling different cultivars that vary widely in yield capability. Caution is suggested in simulating concurrent benefits of thinner leaves (SLA) combined with higher AMAX that may not be realistic, because high AMAX is linked to low SLA in real plants (this combination was not tested in additivity examples for that reason). An uncertainty or concern in our model analyses is that the model currently has a limited number of genetic traits/parameters that can be varied. There is a need for additional model traits (and need for model improvement) to address simulated effects of aspects such as salinity tolerance, water-logging tolerance, leafspot resistance or nematode resistance. There is a future need to link to molecular genetics information and to better test model response to elevated temperatures expected under future climate change.

Uncertainty in the crop model simulation results is also determined by the climate change data outputs of the global climate change models (GCMs) fed to the crop models. While there is uncertainty among GCMs in the future predictions of rainfall, all GCM models predict increase in temperature in future with the increase in greenhouse gases in the atmosphere. To that extent, the crop simulation responses to rising temperature are realistic and generally applicable to all these GCM model outputs. Most GCM models also predict increased frequency of extreme climate events, such as extreme drought or intense rain storms, and changed pest and disease scenarios with climate change. The CROPGRO model for groundnut is currently not sensitive to pest and disease or intense rainfall/water logging and, therefore, needs improvement to enhance its capability. In future, more detailed simulation analysis of climate impacts and evaluation of genetic traits will be needed for spatial visualization to identify regional variations in the technologies needed to cope with climate change.

Conclusions

Groundnut yield response to modification of genetic traits was demonstrated in both current and future growing conditions of target environments in India. Traits such as beginning seed to physiological maturity duration (SD-PM), maximum leaf photosynthesis rate (AMAX), nitrogen mobilization from leaves (NMOB), Seed-filling duration (SFDUR), coefficient for maximum partitioning to pods (XFRT) and turgor-induced shift of partitioning to roots (ATOP) consistently benefitted the crop across environments, while other traits had either negative or positive effects on yield to varying degree depending upon climate and target environment. Enhanced TT of the crop was more beneficial in warmer than in cooler climates. The effect of combining genetic traits on yield was additive and illustrates potential yield improvement possible in new cultivars, assuming that genetic range of traits is well defined. It is concluded from this study that the genetic traits of improved groundnut cultivars need to be optimized to enhance yield and adaptation of the crop considering the current and future climates of the target sites. The CROPGRO model for groundnut can be used to evaluate the potential benefits of genetic traits to guide breeding of improved groundnut varieties. However, the model needs further improvements to assess the impacts of extreme weather events and changed pests and diseases scenarios because of climate change on growth and yield of groundnut crop.

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